Geographical Distribution and Morphological Variability of the Rapid Racerunner, *Eremias velox* (Pallas, 1771) (Reptilia, Lacertidae) in the Eastern Periphery of Its Range

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Abstract Phenotypic traits are usually correlated with the environment where organism occurs. In this study, the distribution of *Eremias velox* in the eastern periphery of its range was specified, and its morphological variation was analyzed. Linear dimensions, pholidosis, coloration and pattern features were compared among 135 specimens from nine populations inhabiting the Balkhash, Ili and Alakol basins, Junggar and Turpan depressions in the territory of Southeast Kazakhstan and Xinjiang, Northwest China. The populations from the Junggar Depression (Kuytun, Shihezi and Urumqi) were characterized by higher mean values of linear characters, the number of scales across the middle of the body and gular, and were similar in the dominant coloration patterns. Small size, dark coloration and almost complete dominance of the striped-type coloration pattern among the specimens from the Alakol Lake islands seem to have an adaptive significance associated with the isolation of the population and type of their habitats. The subspecies *Eremias velox roborowskii* (endemic to the Turpan Depression) is elevated to species level, as supported by morphological divergence congruent with molecular and geographical data, including its peculiar type of coloration pattern, significantly lower amount of femoral pores and a higher percentage of specimens with one enlarged preanal scale (72.7%). These results together confirm a high degree of variability in morphology for *E. velox* in the eastern periphery of its range, reflecting a complex orography and the existence of multiple geographical barriers in this territory.

Keywords *Eremias velox*, Kazakhstan, Xinjiang, habitat, pholidosis, coloration, intraspecies differentiation

1. Introduction

Variation is a central concept in biology (Hallgrímsson and Hall, 2005). Phenotypic variation is the raw material for natural selection, and its unit is the individual, through which fitness is optimized via effects on survival and reproduction. Selective influences and stochastic processes like drift accumulate across individuals, yielding variation at the population level (Lande, 1976). Phenotypic traits are usually correlated with the environment where organism occurs, through effects on physiological, functional and ecological performance (Arnold, 1983). Across populations, phenotypic plasticity and local adaptation are major frameworks for studying associations between the phenotype and the environment, and for elucidating the mechanisms underlying intraspecific phenotypic diversity (Ghalambor *et al.*, 2007; Mullen *et al.*, 2009).

The Rapid Racerunner, *Eremias velox* sensu lato, is one of the most widespread species of the genus *Eremias*. Its range extends from Northern Iran and Afghanistan in the south to the southern boundary of the steppe in Kazakhstan in the north; and from East of Ciscaucasia in the west to Northwest China in the east (Sindaco and Jeremčenko, 2008). The eastern periphery of the species range lies in Southeast Kazakhstan and Xinjiang within the Balkhash-Alakol, Ili, Junggar and Turpan depressions, China (Figure 1; Brushko, 1995; Zhao, 1999; Chirikova, 2007).

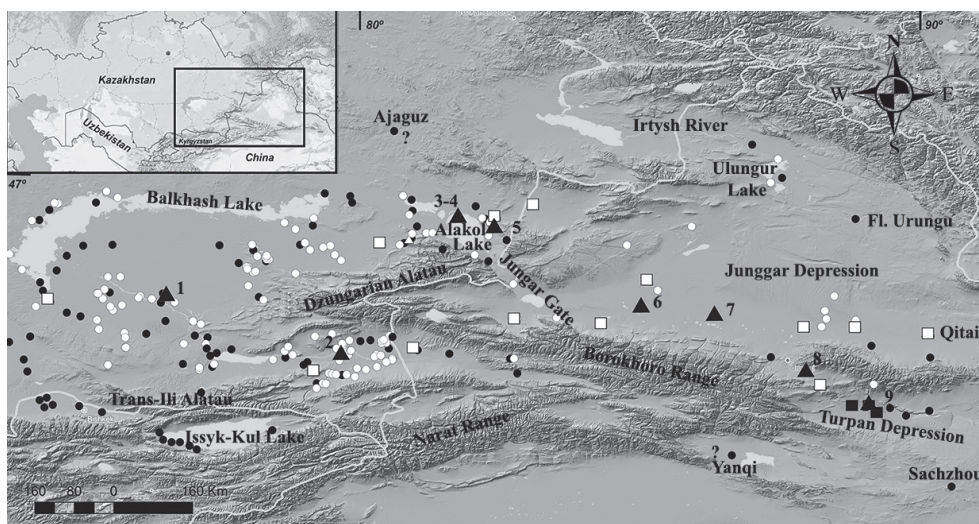Having an extensive range, the Rapid Racerunner

Figure 1 Distribution of the Rapid Racerunner in the eastern periphery of the range. Black triangles: samples studied (1. The right bank of the Ili River, 20 km to the east of Bakanas village; 2. Sands at the confluence of the Charyn River in the Ili River (Charyn); 3. Alakol Lake, Kishkene-Araltobe island, 1970; 4. Alakol Lake, Kishkene-Araltobe island, 2015; 5. 25 km to the southeast of Makanchi village, Barmakkum Sands; 6. Kuytun; 7. Shihezi; 8. Urumqi city suburb; 9. Turpan Depression); Black circles: literature evidence; White circles: new information (2000–2015); White squares: localities, the samples which are grouped in a clade with a nominative subspecies according to the results of molecular genetic analysis (Liu *et al.*, 2014); Black squares: localities, samples which formed a separate clade and were identified as *Eremias velox roborowskii* (Liu *et al.*, 2014).

displays a high morphological variability. Historically, based on the morphological characters, four subspecies are recognized within the species (Szczerbak, 1974; Eremchenko and Panfilov, 1999a; Sindaco and Jeremčenko, 2008): *E. v. velox* (Kazakhstan, Central Asia republics, Dzungaria, Northern Iran); *E. v. caucasia* (Russia: to the south from the lower Volga to the state border, Azerbaijan and Eastern Georgia); *E. v. roborowskii* (China: foothills of western Nanshan, Hami desert, Turpan Depression); and *E. v. borkini* (Kyrgyzstan: Issyk-Kul Depression). Nevertheless, it should be noted that Liu *et al.* (2019) has challenged our understanding of the taxonomy and distribution of different subspecies in *E. velox* sensu lato on the basis of phylogeographical analysis of mtDNA sequences. Thus, one of the relevant issues of the intraspecific taxonomy of *E. velox* sensu lato still remains regarding the taxonomical relation of the populations inhabiting Southeast Kazakhstan and neighboring Xinjiang, China.

The *E. v. roborowskii* subspecies was described by Bedriaga ("1905" 1907) on the basis of the specific coloration patterns among specimens from the "Ssatschsheu" (= Dunhuang, Gansu Province) and "Luk-Tschun" (= Lükqün, Turpan Depression, Xinjiang Uygur Autonomous Region) localities. Later, Boulenger (1921) put *E. v. roborowskii* into the nominative subspecies; but Szczerbak (1974), after repeating the study of lizards from the same areas, confirmed the validity of

the subspecies. Since the holotype was not specified in the original description, Szczerbak distinguished the lectotype and described the series again. According to Szczerbak's data, *E. v. roborowskii* differed from the nominate subspecies in a higher number of gulars and coloration patterns. Exploring the Chinese populations, Szczerbak (1975) noted that there was a significant difference in the number of femoral pores between the samples from the Ssatschsheu and Luk-Tschun, and those from Junggar Depression. However, Wang *et al.* (2014), after an examination of the external morphological characters of the Rapid Racerunners from five localities in Xinjiang (Ili, Turpan and Junggar depressions), did not find any significant differences between them and came to the conclusion that it was necessary to clarify the intraspecific differentiation of *E. velox*.

Molecular genetic analysis of the genus *Eremias* by Wan *et al.* (2007) pointed out the existence of two subspecies in Xinjiang, i.e., the nominative and *roborowskii*; and Rastegar-Pouyani *et al.* (2012) speculated that *roborowskii* could be observed not only in Xinjiang but also in the contiguous territory of Kazakhstan. In the latter case, however, the authors themselves recognized the selective nature of the *roborowskii* clade, which included individuals from populations geographically remote from each other, i.e., from the Aral Sea to East Kazakhstan. Rastegar-Pouyani *et al.* (2012) associated these results with the gene flow

between *roborowskii* and the nominative subspecies. A more recent molecular genetic study using material from the type territory showed that Southeast Kazakhstan is inhabited only by the nominative subspecies; while in Xinjiang *E. v. roborowskii* can also be found alongside the nominative (Liu *et al*., 2014).

Such a disagreement on the taxonomical position of *E. velox* populations from Southeast Kazakhstan and neighboring Xinjiang motivated us to conduct a detailed study of lizard morphological variation, to elucidate its variability and to clarify the taxonomical position of the certain populations. First, we implemented an analysis of geographical distribution of this species in the eastern part of its range to reveal the isolated populations and to check whether there is some exchange between them. Second, we evaluated the variability of the morphological characters for these populations, considering a sexual dimorphism, an inter-character correlation and substrate preferences of the lizards. We also examined a possible association of phenotypic variation with geographical isolation, with special attention to the most remote and isolated population from the Turpan Depression in Xinjiang.

2. Materials and Methods

2.1. Distribution A map with the occurrences of *E. velox* was constructed in the ArcMap environment to analyze the distribution of the Rapid Racerunner (Figure 1). The basis of the map was literary materials (Szczerbak, 1974; Yao, 1983; Zhao, 1985; Wang and Autumn, 1990; Brushko, 1995; Dai *et al*., 2004; Chirikova, 2007; Wan *et al*., 2007; Liu *et al*., 2014; Wang *et al*., 2014), supplemented by information from the collections of the Chengdu Institute of Biology (CIB) and the Institute of Zoology of the Republic of Kazakhstan, as well as data personally collected during field survey in 2013–2015. The geographical coordinates of the localities of lizard finds were determined with GPS (recent data) or restored by topographical maps (old data).

2.2. Morphology For exploring morphological variability of *E. velox* in the eastern periphery of its range, we sampled a total of nine populations in the intermountain and foothill depressions of Xinjiang and Southeast Kazakhstan (Figure 1): 1. the right bank of the Ili River, 20 km to the east of Bakanas village (12 males) (Bakanas); 2. sands at the confluence of the Charyn River in the Ili River (Charyn) (6 males, 14 females); 3. Alakol Lake, Kishkene-Araltobe island, 1970 (15 males, 6 females); 4. Alakol Lake, Kishkene-Araltobe island,

2015 (11 males, 3 females); 5. 25 km to the southeast of Makanchi village, Barmakkum Sands (Makanchi) (11 males, 6 females); 6. Kuytun (6 males); 7. Shihezi (8 males, 6 females); 8. Urumqi city suburb (8 males, 4 females); 9. Turpan Depression (19 males) (see Appendix 1).

To characterize morphological diversity within and divergence across populations, we considered 12 morphological characters, which have been extensively used for the systematics of the genus *Eremias* (e.g., Szczerbak, 1974): 1. L. (Longitudo corporis) – snout-vent length; 2. L.cd. (Longitudo caudalis) – tail length (from cloaca to the tip of the tail); 3. L.c. (Longitudo capitis) – head length; 4. Lt.c. (Latitudo capitis) – head width; 5. P.p. (Pes posterior) – hind limb length (from the glenoacetobular cavity to the base of the claw of the 4th finger); 6. Sq. (Squamae) – the number of scales around midbody; 7. Ventr. (Ventralia) – the number of transverse rows of thoracic and abdominal scales; 8. G. (Gularia) – the number of gular scales along mid-line of throat; 9. P.fm. (Pori femoralis) – the number of femoral pores; 10. Sq.cd (Squamae caudalis) – the number of scales around the 9–10th tail ring; 11. the number of enlarged preanal scales; 12. the characters of the head pholidosis, with a special attention to presence/absence of the granules around the supraoculars, which demonstrating a geographic variability (Chirikova, 2004).

Different coloration patterns were identified on the basis of the location of the spots, their sizes, as well as the stripes on the upper back and size and the location of pigmented spots on the sides of the trunk. For comparison between the populations, the male individuals were used. To calculate the similarity of populations by phenes (coloration patterns in our case), the index proposed by Zhivotovsky (1982) was used, which has been successfully applied for phenotypic comparison in other vertebrate groups (e.g., Korablev *et al*., 2011; Korablev *et al*., 2014).

$r = \sqrt{p_1 q_1} + \sqrt{p_2 q_2} + \sqrt{p_m q_m}$, where *r* is the population similarity index, and *p* is the frequency of the phene in the first population, and *q* is the frequency of the phene in the second population, and *m* is the number of phenes.

2.3. Statistical analysis Statistical analyses were performed using the STATISTICA 10 software (Statsoft, 1999–2019). The critical value of statistical significance when checking for null hypothesis was set at 0.05. If the significance value of the statistical criterion for the measure was exceeded, the null hypothesis was applied. The normality of the distribution of quantitative

characters in the separate comparison groups was checked using the statistical criteria of the Kolmogorov-Smirnov and Shapiro-Wilk tests. Both tests are capable of revealing significant differences between the pattern of character distribution and the normal distribution model wherein Shapiro-Wilk test is especially powerful to check the normal distribution in the limited samples (Kendall and Stuart, 1973; Afifi and Azen, 1982). The hypothesis of normality of the distribution is accepted if the criterion gives a value of more than 0.05 in a particular subgroup of observations. Arithmetical means and mean squares (standard) of errors of mean, as well as the coefficient of variation, are calculated for all the quantitative characters in the comparison groups. The mean values and confidence intervals are presented in graphical form. Descriptive statistics are presented in the text as $X \pm SE$, where X is the mean, and the SE is standard error of mean. To compare the central characters of the groups, parametric and nonparametric methods were used: ANOVA analysis of variance, including by means of the Kruskal-Wallis test and Wilcoxon signed-rank test, median test and the Van-der Waerden test (Kendall and Stuart, 1973; Afifi and Azen, 1982; Kim *et al.*, 1989). To assess the correlation between a pair of quantitative indicators, Pearson and Spearman correlation coefficients were used. A scatterplot was used for the graphical presentation.

A cluster exploratory analysis was undertaken, which main aim was to identify latent groups of observation (Ledermann and Lloyd, 1984; Kim *et al.*, 1989). The cluster analysis is to split a set of observed objects and characters into different groups or clusters so that the members of each group are similar to one another. Given the differences in the scales of the analyzed characters, all the quantitative characters were transformed into one standard form before conducting the cluster analysis. As a result, all the characters in the new scales had zero mean and standard deviation equaled to one. A hierarchical clustering algorithm was used to conduct a cluster analysis with these new variables. Hierarchical cluster analysis with a dendrogram allowed the number of allocated clusters to be visually determined. In both cases, the Ward's algorithm was used (Kim *et al.*, 1989) and the Euclidean metric was applied (Ledermann and Lloyd, 1984; Kim *et al.*, 1989).

3. Results

3.1. Distribution and habitats The Rapid Racerunner is widespread in Southeast Kazakhstan, North and East

Xinjiang (Figure 1). During field studies, we recorded encountering *E. velox* in the Balkhash, Alakol and Ili depressions, Sogetinsk plain, Junggar Gate, Junggar Depression as well as the southern foothills of Bogda Shan range at the periphery of the Turpan Depression.

The dominant type of biotope for the Rapid Racerunner in Southeast Kazakhstan, North and East Xinjiang can be categorized as fixed sands and the surrounding clay plains. This is present in the Alakol Depression (Makanchi) in the pit-and-mound sands with *Artemisia* sp*., Astragalus* sp. and gramineous plants; in the Ili Depression (Charyn) – at pit-and-mound sands with bushes *Haloxilon* sp. and *Calligonum* sp. and at salt marshes in the lowlands.

In the Shihezi area (in the Junggar Depression), the Rapid Racerunner inhabits small areas of fixed sands with *Haloxylon* sp*., Ceratoides* sp. and *Artemisia* sp. bushes and at the clay salt marshes in the lower parts between the barchans; and in Kuytun – at the ridged barchans and in the lower parts between the barchans with *Haloxylon* sp. and *Artemisia* sp. In the Turpan Depression, the biotopes of the Racerunners are represented by the sandy-loessic and gravel-loessic plains (type territory: Shanshan County), low barchans with fine gravel and *Calligonum* sp*., Alhagi* sp*., Tamarix* sp. and *Haloxylon* sp. for the dominants, at the foot of the mountains – Gobi-type gravel deserts. The racerunners' habitats in Xinjiang were fragmented drastically due to industrial activity.

On the islands of Lake Alakol, the Racerunner inhabits rubble-loam plains and sabulous-rocky slopes of low hills with vegetation of *Artemisia* sp., *Atraphaxis* sp., *Salsola* sp. and gramineous plants in different combinations (Kubykin, 1975; our data). The ground has a darker coloring because of the typical desert ground conditions forming its rubble-rocky soil.

3.2. Morphological analysis A test of the hypothesis of normality showed that most of the morphological characters had a normal distribution. The results of the test are given in Table 1. The Shapiro-Wilk test, as the most reliable statistic criterion for small number of observations, revealed the normal distribution for L., L.cd. and P.fm. for all the samples. The Shapiro-Wilk test rejected the hypothesis of normal distribution for L.c. (No. 6), Lt.c. (No. 9), L.p. (Nos. 8, 9), Sq. (No. 4), Ventr. (Nos. 2, 3, 5), G. (No. 8), Sq.cd. (No. 6). Since for the other characters the normal distribution was not detected for all samples, we used both parametric and non-parametric methods of analysis.

3.2.1. Sexual dimorphism Significant differences (P = 0.0002, P = 0.0001) between males and females were identified for the linear biometric characters such as the

head length and width, the hind limb length. The diagram showing the sexual dimorphism of linear and pholidosis characters is presented in Figure 2. Males had higher values for the mentioned characters. In addition, males had a greater relative length of hind limbs ($P = 0.01$) and tail ($P = 0.001$).

The scalation (pholidosis) characters in our samples did not exhibit significant sexual differences. Previously, when describing the *E. v. velox* and *E. v. caucasia* subspecies, Szczerbak (1974) noted sexual dimorphism for Ventr. and Sq.cd. and in his later work (Scerbak [= Szczerbak], 1981) for Sq. and P.fm. Sexual dimorphism was observed in the coloration patterns on the upper and side parts of the torso. Over 80% of females had light-colored stripes on their back. We have not observed specimens with pigmented spots on the back. The upper row of white pigmented spots, which on some specimens merged into stripes, was vaguely seen on the sides of the torso. The bottom row of colored pigmented spots was weakly pronounced and could be seen reaching only the middle of the side. The coloration pattern on the backs of the males significantly varied and usually took the shape of spots. The rows of pronounced white and colorful spots on the sides of the torso reached the base of the thighs.

3.2.2. Correlation of characters A positive correlation among all linear biometric characters was observed in
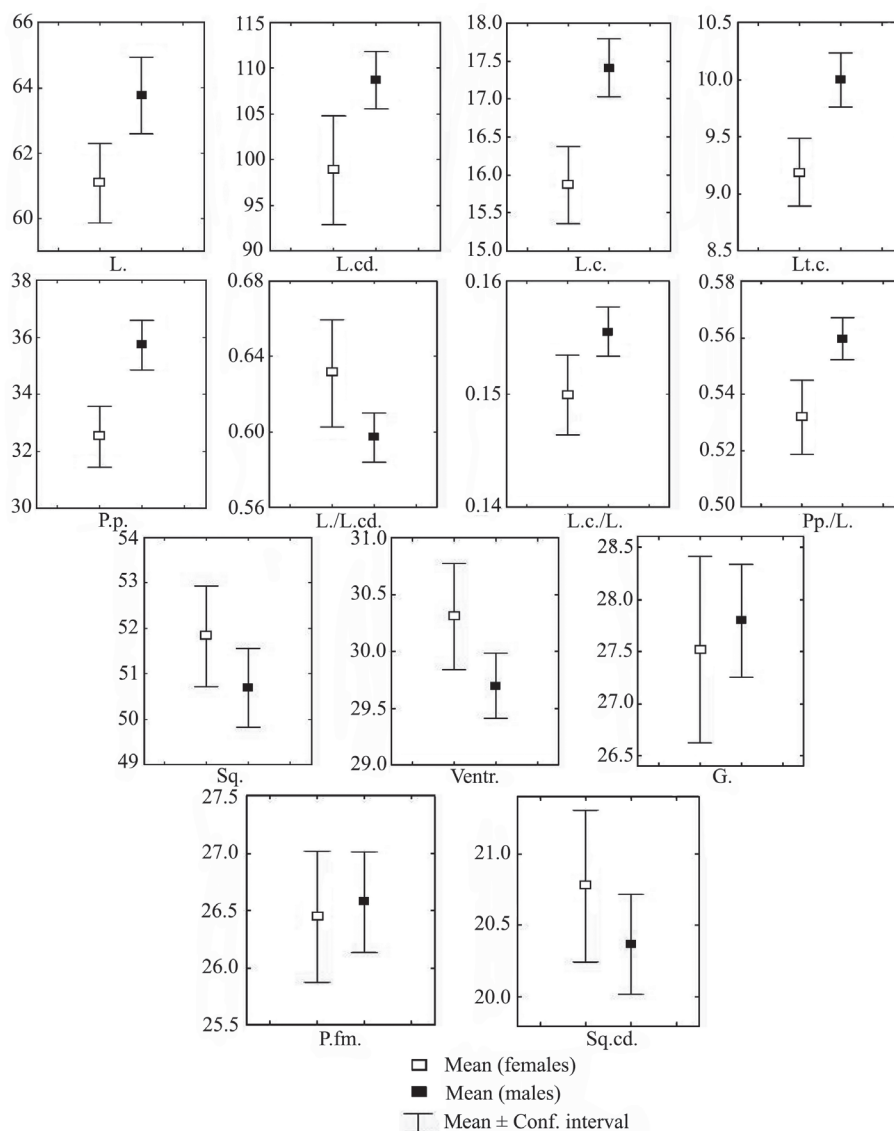
Figure 2 Sexual dimorphism in linear and pholidosis characters of *Eremias velox*. L.: snout-vent length; L.cd.: tail length; L.c.: head length; Lt.c.: head width; P.p.: hind limb length; Sq.: the number of scales around midbody; Ventr.: the number of transverse rows of thoracic and abdominal scales; G.: the number of gular scales along mid-line of throat; P.fm.: the number of femoral pores; Sq.cd: the number of scales around the 9–10th tail ring.

both sexes. The values of the Spearman and Pearson coefficients are listed in Table 2. The correlation among the scalation characters was either very weak or absent. Characters correlation analysis in each population confirmed the presence of positive correlation between linear biometric characters in all the populations. Analysis of the scalation characters demonstrated a weak correlation between Sq. and G. (on both coefficients) and Sq. and Sq.cd. (on Spearman). As an example, we provided the scatterplot with relationship between L. and L.c. and between Sq. and G. in Figure 3.

3.2.3. Variability of linear biometric characters Given pronounced sexual dimorphism across the linear biometric characters, we have conducted comparison only among males. We have provided differences in the size of specimens from different populations. However, these differences did not reach a statistically significant level (P

> 0.05). Specimens from Bakanas (No. 1) demonstrated high average values on linear biometric characters, as well as specimens from Xinjiang (Nos. 6–9) (Figure 4A, C, D).

3.2.4. Variability of scalation characters Although our material did not exhibit statistically significant sexual differences in pholidosis, we took into account data from previous researchers (Szczerbak, 1974; Scerbak [= Szczerbak], 1981; Shammakov, 1981) and considered only males.

The majority of the scalation characters from Southeast Kazakhstan and Xinjiang was considered to be overlapping with each other; but there were some differences. The comparison showed that the Xinjiang racerunners (excluding the Turpan samples) had a higher count of Sq. (54.8–55.7) in comparison with others (46.5–52.1). Specimens from the Turpan (No. 9) had statistically

Table 1 Test of normality of distribution of the morphological characters studied.

Feature	Number of subgroups for comparison (geographic samples)	General number of normality hypothesis for verification	Number of accepted hypothesis of normality according to Kolmogorov-Smirnov test	Number of accepted hypothesis of normality according to Shapiro-Wilk test
L.	9	9	8	9
L.cd.	9	9	9	9
L.c.	9	9	7	8
Lt.c.	9	9	7	8
P.p.	9	9	8	7
Sq.	9	9	8	8
Ventr.	9	9	7	6
G.	9	9	9	8
P.fm.	9	9	8	9
Sq.cd	9	9	5	6

L.: snout-vent length; L.cd.: tail length; L.c.: head length; Lt.c.: head width; P.p.: hind limb length; Sq.: the number of scales around midbody; Ventr.: the number of transverse rows of thoracic and abdominal scales; G.: the number of gular scales along mid-line of throat; P.fm.: the number of femoral pores; Sq.cd: the number of scales around the 9–10th tail ring.
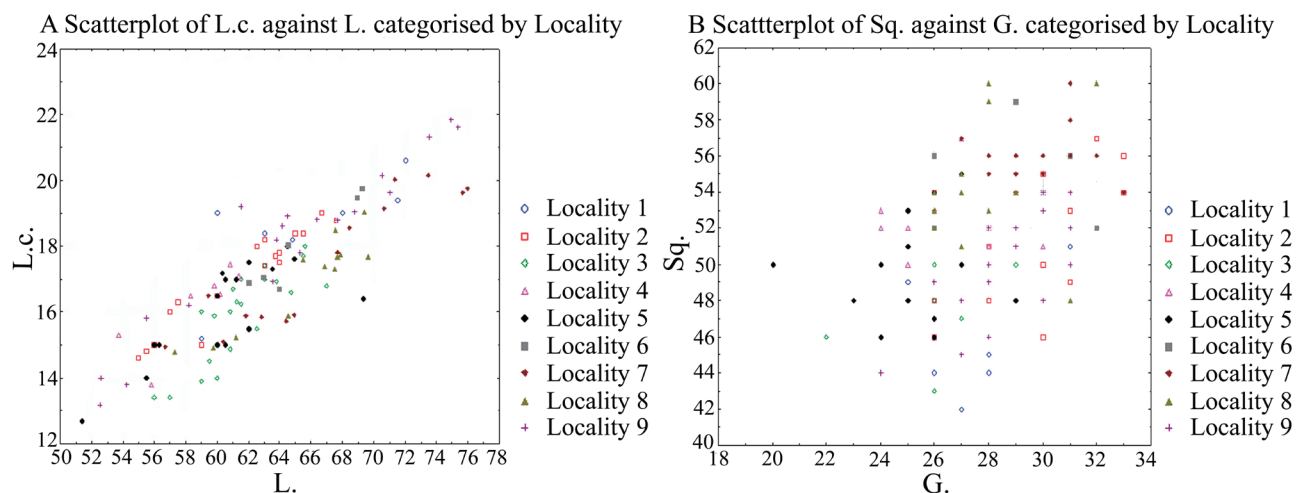
Figure 3 Example of correlation of linear (A) and pholidosis (B) characters in the studied samples of *Eremias velox*. L.: snout-vent length; L.c.: head length; Sq.: the number of scales around midbody; G.: the number of gular scales along mid-line of throat.

Figure 4 Variability of linear (A–D) and pholidosis (E–H) characters of male *Eremias velox*. L.: snout-vent length; L.cd.: tail length; L.c.: head length; P.p.: hind limb length; Sq.: the number of scales around midbody; G.: the number of gular scales along mid-line of throat; P.fm.: the number of femoral pores; Sq.cd: the number of scales around the 9–10th tail ring.
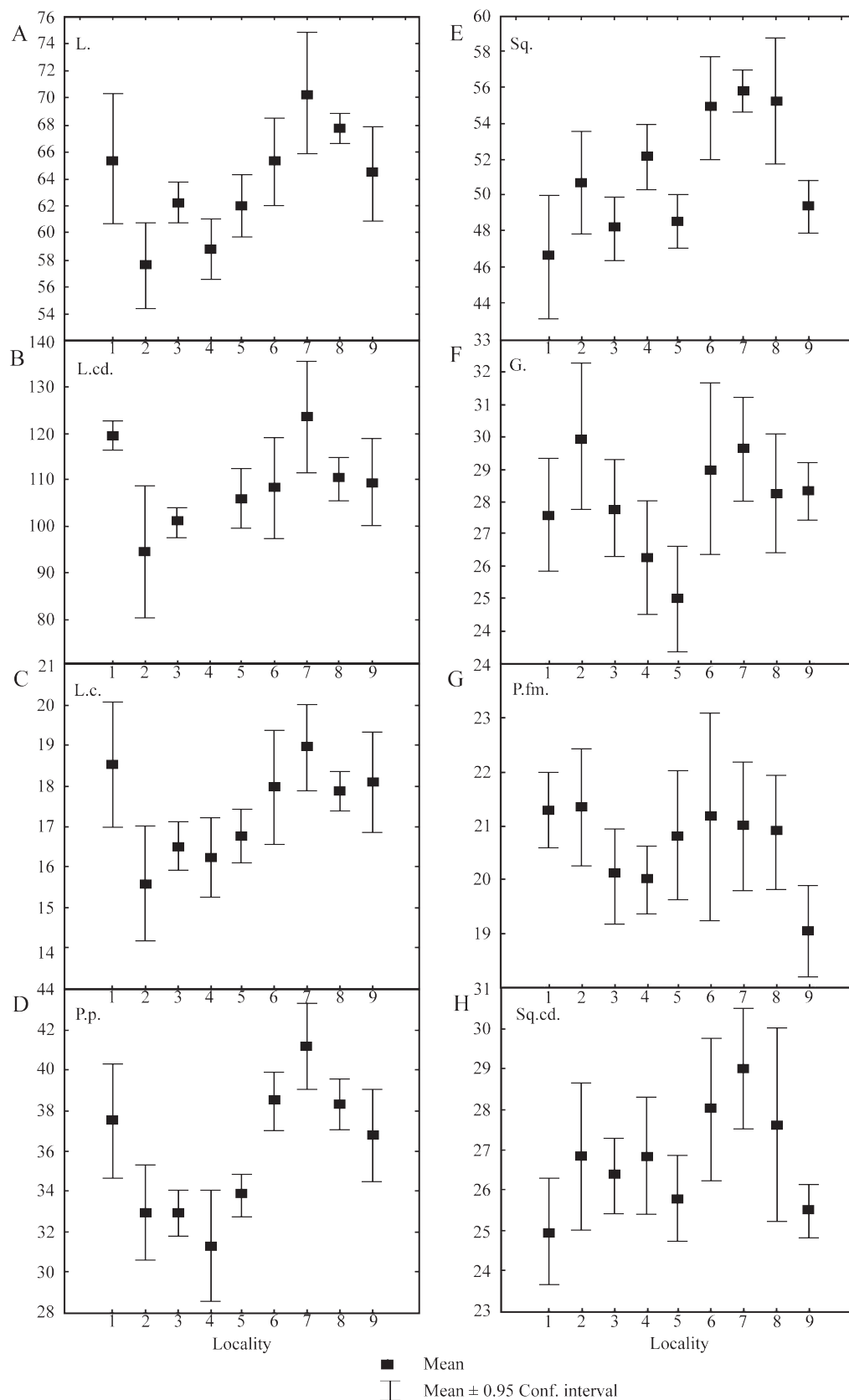
lower counts for this trait: 49.36 (*P* = 0.0001: Figure 4E). A higher count of G. (28.2–29.6), in comparison with populations in Kazakhstan (25.0–27.57) excluding Charyn, was observed among all populations in Xinjiang. However, this difference was statistically significant only when conducting pair-wise comparison of specimens from Shihezi and Makanchi (*P* = 0.0008), and Turpan and Makanchi (*P* = 0.002) (Figure 4F). In the Kazakhstan populations, the highest count for gular scales was observed among specimens from Charyn, but only when conducting pair-wise comparison with the Makanchi specimens (*P* = 0.002). Additional analysis of six specimens from the Horgos population (geographically located between the populations from Charyn and Xinjiang), did not reveal a high average count for G.; but there were individuals with the maximum G. count [26–33 (27 ± 1.11)]. The Xinjiang populations (Nos. 6–8) differed, with higher counts of mean Sq.cd. (27.6–29) compared to the rest of the populations (25–26.8), although the difference was not statistically significant. Specimens from the Lake Alakol islands (Nos. 3–4) and Turpan were characterized by low average values of

femoral pores (20.06, 20.0 and 19.05, respectively; Figure 4G).

Analysis of the discrete scalation characters of the head and preanal area showed differences between specimens on two characters – the shield pattern in the preanal area and the presence or absence of granules around supraocular (Table 3, Figure 5). 72.7% of the Turpan racerunners had one enlarged preanal scale. Specimens from most populations had an incomplete row of granules scales between the supraocular and frontal scales. The largest number of specimens with the full row of granules was observed in the Bakanas population (No. 1); the prefrontal scales of specimens from Turpan (No. 9) and the Lake Alakol islands (No. 3) were not separated by the granules (43.75%; Table 3). The remaining percentage of specimens, whose frontal scale was not separated by the granules, amounted to 0–22.2%.

Cluster analysis of five scalation characters (Sq., G., P.fm., Sq.cd, Ventr.) showed that there was no clear differentiation between the studied populations (Figure 6). All clusters comprised specimens of various populations that were presented in different proportions. However,

Table 2 Correlation of morphological characters of *Eremias velox* (characters with a correlation equaling to *P*<0.0001 are given in bold)

	The Pearson Coefficient									
	L.	L.cd.	L.c.	Lt.c.	P.p.	S.q.	Ventr.	G.	P.fm.	Sq.cd.
L.		**0.6874**	**0.8636**	**0.81489**	**0.82257**	0.22737	–0.079	0.26354	0.195	0.166
L.cd.	**0.6672**		**0.7914**	**0.76898**	**0.76824**	0.1394	–0.2	0.30888	0.303	0.21833
L.c.	**0.8452**	**0.8141**		**0.91565**	**0.86151**	0.13142	–0.25776	0.30835	0.2053	0.16397
Lt.c.	**0.7958**	**0.7959**	**0.92583**		**0.83648**	0.12372	–0.30136	0.2669	0.24729	0.14229
P.p.	**0.806**	**0.773**	**0.8692**	**0.84019**		0.25816	–0.1573	**0.42465**	0.24247	0.276
Sq.	0.2153	0.1487	0.13188	0.2566	0.2566		0.34292	**0.43219**	0.20051	0.44809
Ventr.	–0.1112	–0.2288	–0.2799	–0.3341	–0.19995	0.27971		0.17201	0.1352	0.2029
G.	0.2857	0.2876	0.3146	0.28035	0.42006	**0.43737**	0.12856		0.21955	0.22901
P.fm.	0.1912	0.2994	0.20113	0.18263	0.2403	0.21035	0.1289	0.21453		0.31807
Sq.cd.	0.1487	0.2221	0.18644	0.136	0.25395	**0.44363**	0.21509	0.24274	0.3211	

(left vertical label: Spearman coefficient, significance level)

L.: snout-vent length; L.cd.: tail length; L.c.: head length; Lt.c.: head width; P.p.: hind limb length; Sq.: the number of scales around midbody; Ventr.: the number of transverse rows of thoracic and abdominal scales; G.: the number of gular scales along mid-line of throat; P.fm.: the number of femoral pores; Sq.cd: the number of scales around the 9–10th tail ring.
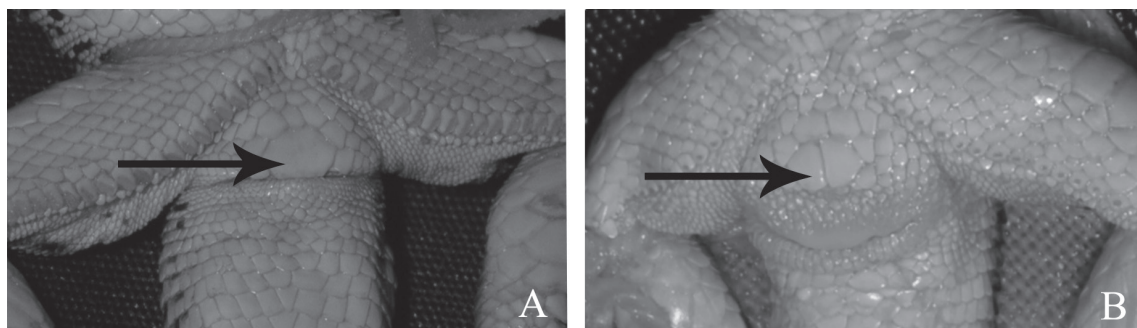

Figure 5 Preanal area shield pattern variations among the Rapid Racerunners from the eastern periphery of the range: A: one enlarged preanal scale; B: two enlarged preanal scales.

Xinjiang populations made up more than half of the first cluster: 66% if including the Turpan specimens, while 54% if excluding the Turpan samples. The second cluster was represented by two subclusters. In addition to the above, specimens from the Lake Alakol islands (38.6%) made up the majority of the first subcluster (I); and in the second subcluster (II) there were more specimens from the Turpan Depression (35.7%) (Figure 6).

Table 3 Variability of pholidosis of the head and preanal area for male *Eremias velox*. See Materials and Methods for the population number.

| Name of the character	Population number								
	1	2	3	4	5	6	7	8	9
One enlarged preanal scale	33.33	10.5	11.76	16.66	5.26	0	10	16.66	72.72
Two enlarged preanal scales	60	73.7	76.48	66.67	68.42	100	60	66.68	27.27
No enlarged preanal scales	0	15.8	11.76	0	26.31	0	30	16.66	0
One enlarged split preanal scale	6.67	0	0	16.66	0	0	0	0	0
Supraocular scales are separated from the frontal scale by:									
– complete number of beads,	40	30	12.5	0	9.5	0	0	5.55	6.25
– incomplete number of beads,	40	30	0	42	38.1	50	69.23	55.55	12.5
– one bead	23.3	40	43.75	50	38.1	50	30.76	16.66	37.5
Supraocular scales are not separated from the frontal scale	10	0	43.75	7.2	14.3	0	0	22.22	43.75
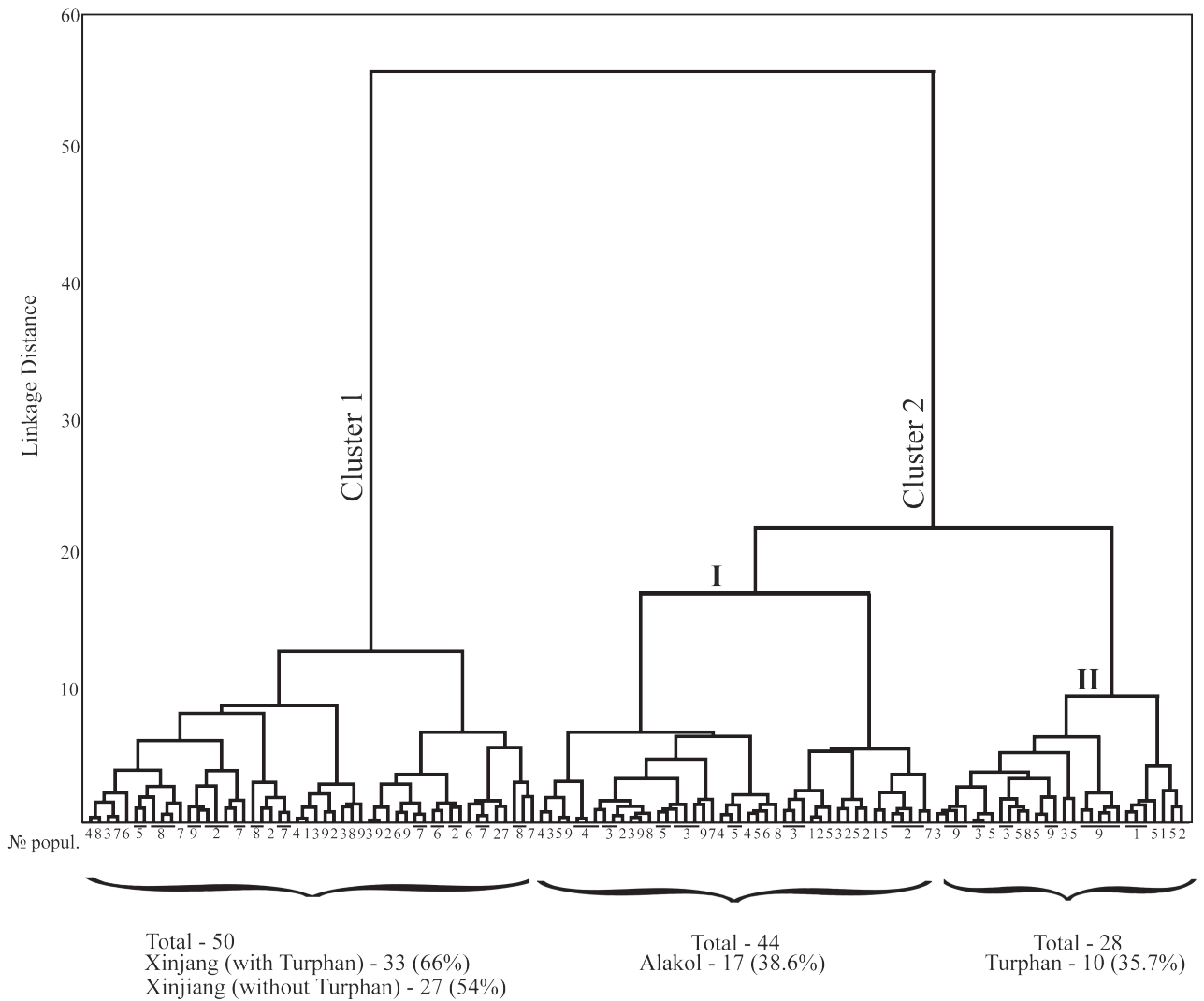
Figure 6 Cluster analysis of five pholidosis characters of *Eremias velox*.

3.2.5. Variability of coloration pattern   Coloration and its pattern play an important role in studies of the intraspecific taxonomy of *E. velox*. The back-coloration pattern of the nominate subspecies is characterized by the presence of variations such as one or three longitudinal dark stripes of contrasting colors, longitudinal intermittent stripes or rows of spots, and dark dots and spots. The sides of the torso often have two rows of pigmented spots, but it is not always the case. The pigmented spots of the bottom row are blue, green or light grey.

In the specimens studied, we identified 12 types of dorsal coloration patterns (Figure 7; Table 4): (1) a broad dark-brown streak between two light-colored stripes on the back; (2) large dark spots between two light-colored stripes on the back; (3) small dark spots on light-colored stripes on the back; (4) dark spots located both on the light-colored stripes on the back and between them, as well as dark spots from the edges of the pigmented spots on the sides reaching the light stripes on the back; (5) dark spots, often elongated in the transverse direction, located across the back; (6) numerous small spots and dashes on the back; (7) dark spots grouped along the light stripes; (8) light stripes split into elongated spots; (9) two rows of pronounced pigmented spots; (10) light stripes absent and the coloration in the form of occasional small specks or dots; (11) similar to type 2, but all dark elements of coloration poorly pronounced; (12) very rare dots between the light stripes.

As shown in Table 4, 11 types of coloration pattern were observed among males, and nine types were noted among females. At the same time, except for a quarter of females from Urumqi (No. 8), in all other populations, only males had the types of coloration patterns without stripes or with weakly pronounced stripes: spotted, speckled and dotted patterns (Figure 7: 4, 5, 6 and 9; Table 4).

A relatively high diversity in coloration pattern was noted among most of the males, only except for some populations from the Lake Alakol islands, Shihezi and Turpan, in the studied populations, as well as across the populations (Table 4). The males from the Lake Alakol islands, Shihezi and Turpan in contrast demonstrated high uniformity of the pattern at intra-population level. The females of Alakol islands and Makanchi samples shared
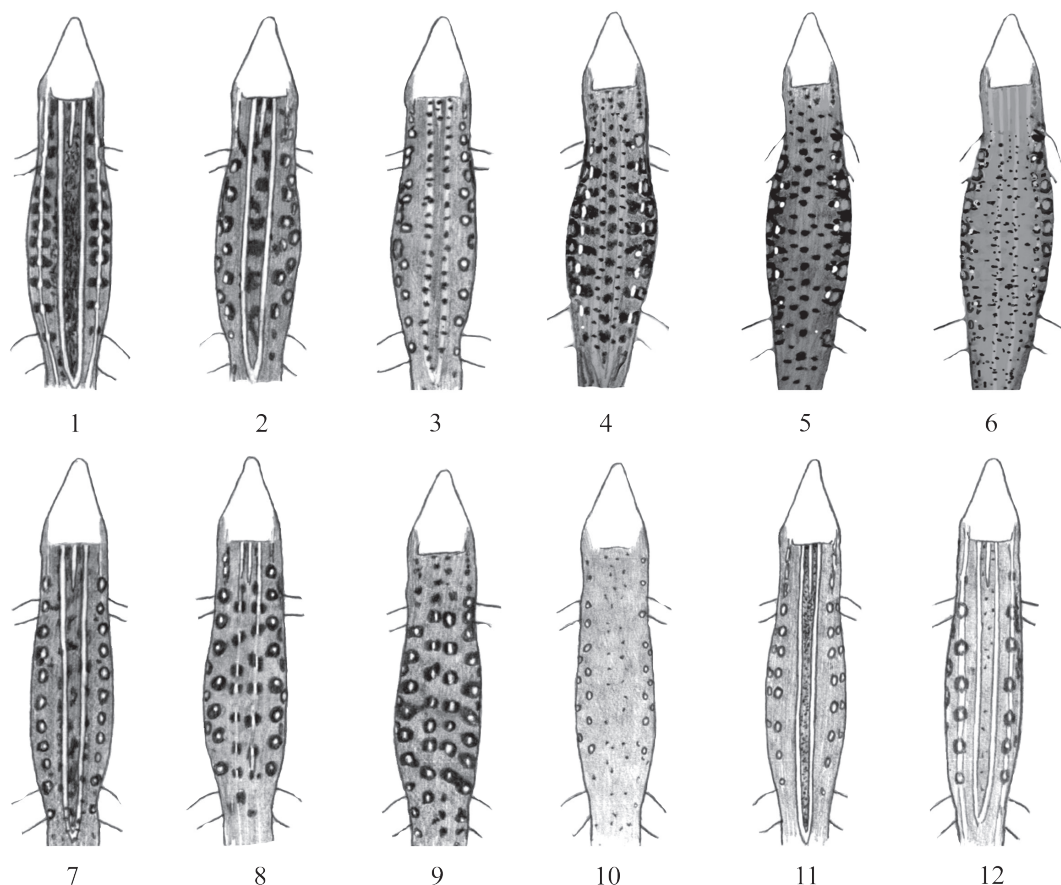

Figure 7 Variation of the coloration patterns on the upper torso of *Eremias velox* in the eastern periphery of the species range.

high uniformity of patterns (Table 4). Male individuals from the Alakol islands, collected in different periods, showed a high similarity between each other ($r = 0.9$) and, to a lesser extent, with the geographically nearest population of Makanchi ($r = 0.74$) (Table 5). The Turpan individuals differed with a peculiar pattern, which was not registered in any other studied populations.

Specimens with a pattern having pigmented spots along the middle of the back dominated among the males of four populations (Bakanas, Charyn, Kuytun and Shihezi: Nos. 1, 2, 6 and 7, respectively), and other types of pattern were dominant in the remaining populations (Figure 7: 9; Table 4). The similarity index (r) for the coloration patterns among the populations compared ranged from 0.57 to 0.82 (Table 5). The bottom row of blue and green spots was well pronounced only up to the middle of the body among the majority of adult specimens from the populations. The main background of the body was gray or grayish-brown.

In the populations from the Lake Alakol islands (Nos. 3–4), collected at different times, specimens of both sexes were characterized by a dark-grey background to the upper torso and a striped pattern (Figure 7: 1). Among some males and females, the top row of side spots on the torso took a shape of a light-colored stripe, the appearance of which varied between different individuals. There were no spots on the pileus.

Specimens from the Turpan Depression had a peculiar type of coloration pattern. The upper part of the back for the males was covered with many spots; and most spots were randomly scattered and elongated in the transverse direction (Figure 7: 5 and 6; Table 4). The coloration pattern on the sides had white spots surrounded by large black spots on the upper row and large blue spots on the bottom row, which almost reached the hind limbs. Our calculations indicated that the largeness of the blue spots was determined by the scale counts that make them up, compared to specimens from other sites. Thus, for the Turpan specimens, the blue spots on the middle of the torso were composed of at least 10 scales, while the count for the specimens from other sites was 2–8 scales. And the spots in the forelimbs area covered 20–40 and 12–20 scales, respectively. The Turpan specimens were distinguished by rust-brown coloration of the upper torso and absence of bright distinct spots on the pileus.

4. Discussion

4.1. Distribution Our field data showed that *E. velox*

Table 4 Occurrence of different types of coloration patterns of *Eremias velox* in the studied populations (in %). See Materials and Methods for the sample number. Types of coloration patterns refer to Figure 7.

Coloration pattern	Populations																	
	Males									Females								
	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
1	–	–	81.5	100	23	16.6	–	–	5.88	–	–	100	100	–	–	–	25	–
2	–	27.3	12.5	–	46.4	33.4	–	25	5.88	–	–	–	–	90	–	–	–	-
3	–	27.3	–	–	7.6	–	–	37.3	–	–	25	–	–	–	–	33.4	–	–
4	–	–	–	–	–	–	–	12.5	5.88	–	–	–	–	–	–	–	25	–
5	–	–	–	–	–	–	–	–	70.6	–	–	–	–	–	–	–	–	–
6	–	–	–	–	–	–	–	–	11.76	–	–	–	–	–	–	–	–	–
7	25	–	–	–	15.4	–	–	12.5	–	–	25	–	–	–	–	–	–	–
8	–	9.1	6	–	7.6	–	14.28	–	–	–	–	–	–	–	–	50	–	–
9	50	36.76	–	–	–	50	85.72	12.5	–	–	–	–	–	–	–	–	–	–
10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	25	-
11	12.5	–	–	–	–	–	–	–	–	–	25	–	–	10	–	–	25	–
12	12.5	–	–	–	–	–	–	–	–	–	25	–	–	–	–	16.6	–	-

Table 5 Similarity of samples by coloration pattern (males).

	1	2	3	4	5	6	7	8	9
1		0.42	0	0	0.19	0.5	0.65	0.43	0
2			0.57	0	0.82	0.73	0.67	0.79	0.13
3				0.9	0.74	0.57	0.09	0.18	0.3
4					0.48	0.41	0	0	0.24
5						0.59	0.1	0.65	0.28
6							0.65	0.54	0.24
7								0.33	0
8									0.21

has more dense spatial distribution within the eastern periphery of the species range than it was recognized before (Figure 1). The most northern *E. velox* found in the eastern periphery of the range was known from the collections of A. A. Kushakevich (ZISP No. 6837) in the Sergiopole suburbs (now Ayaguz town) (Nikolsky, 1905). Our survey of the territory led us to assume that this finding does not belong to the city suburbs with a steppe-type landscape, but to the valley of the southern course of the river with the same name, where on the left bank Karakum sands are located. Thus, the northern boundary of the *E. velox* distribution in the eastern periphery of the range in the Kazakhstani territory lies within the northern border of the Balkhash and Alakol basins (Figure 1).

The most reliable northern, eastern and southern records of *E. velox* in the eastern periphery of the species range, except for *E. v. borkini* in the Issyk-Kul Depression, lie in Xinjiang (Figure 1). They come from Buerjin at the Black Irtysh River (Shi *et al*., 2002; Wan *et al*., 2007); the Ulungur Lake Basin (first finds in 1878–1879 [Potanin, ZISP No. 5173 and Przhewalsky, ZISP No. 6548: Szczerbak, 1974] confirmed by us in 2014); Qitai County (Wan *et al*., 2007; Liu *et al*., 2014) and the Turpan Depression, where, since the first discoveries in 1895 (Roborowski and Kozlov, ZISP Nos. 9130, 9132: Szczerbak, 1974), the presence of a resident population was registered repeatedly (Wang and Autumn, 1990; Shi *et al*., 2002; Liu *et al*., 2014; Wang *et al*., 2014). The northern boundary of the distribution of *E. velox* in the eastern periphery of the range generally coincides with the northern border of the desert landscape zone, occupying the Southeast Kazakhstan and Xinjiang on 46°40'–47°40' N (Zaychikov, 1964; Medeu, 2010).

It is necessary to dwell on some dubious records of racerunners found far from the described areas of Xinjiang and identified as *E. velox*. The Ssatschsheu (= Dunhuang) locality (1894, Roborowsky and Kozlov, ZISP No. 9198: Nikolsky, 1905) is probably an error for *E. velox* because numerous new racerunner collections from the Dunhuang region have produced only *Eremias vermiculata*. By reasoning similar to that in Macey *et al*. (1997) on *Teratoscincus roborowskii*, the only record labeled from Dunhuang is probably the result of mixing of museum labels during examination of specimens collected by the Russian Geographic Society Expedition to Central Asia in 1893–1895 under the leadership of V.I. Roborowski (Kozlov, 1899). The route of this expedition (Figure 6 in Macey *et al*., 1997) passed through the Turpan Depression in September 1893 and September 1895. The expedition stayed in Ssatschsheu (Dunhuang)

during the spring of 1894. We suggest that the specimen ZISP No. 9138 could have been collected together with ZISP No. 9130 and ZISP No. 9132 by V.I. Roborowski and P.K. Kozlov during the last part of their expedition between the Hami Oasis and Turpan Depression. It should be mentioned that Yao (1983) documented the Rapid Racerunner in the vicinity of Dunhuang in Gansu Province, China. It is most probable that some individuals of *E. vermiculata* were incorrectly assigned to *E. velox* in Yao (1983). Zhao's (1985) finding of *E. velox* in the Tarim Basin (Lop, Hotan and Yecheng), according to Eremchenko and Panfilov (1999b), appeared to result from his inability to distinguish between *E. velox* and *Eremias buechneri*. Surprisingly, the specimen (voucher number CIB3558) from Yanqi County in Xinjiang was recorded as *E. velox* in Dai *et al*. (2006). After carefully revisiting that specimen (CIB3558), we confirmed its identity to be *Eremias multiocellata* complex rather than *E. velox*.

According to the updated data, the eastern periphery of *E. velox* range is limited to the northern borders of the Balkhash and Alakol basins and the valley of the Black Irtysh River in the north; the eastern borders of the Junggar and Turpan depressions in the east; and the northern foothills of the Tian Shan – Borohoro, Ketmen and Trans-Ili Alatau in the south.

In our opinion, at least four geographically isolated populations with different levels of isolation can be distinguished within the area described. One of them inhabits the Turpan Depression, which has undergone a deepening isolation since Neogene (Murzayev, 1966). This population is separated from the species' main range by extreme eastern spurs of the Eastern Tien Shan – Borokhoro, Iren-Khabyrga, Jarges and Bogda-Shan (or Bogda-Ula) ridges. The second isolated population inhabits the Junggar Depression surrounded by the ridges of different mountain systems and formed in Late Pliocene and Pleistocene (Mamedov and Novikov, 2015). There are some ways of possible contact between the populations of the Junggar Depression, Balkhash and Alakol basins. There are the Junggar Gate and the intermountain depression between the Urkashar and Birliktau mountains. The third isolated population inhabits one of the islands of Alakol Lake. It has very recent appearance because the island itself was formed no more than 150 years ago (Kurdukov, 1951). The fourth exists in Issyk-Kul Lake Basin. It is separated from main species range by the ridges of the Northern Tien-Shan, which has acquired its highland appearance in Middle Pliocene (Burtman, 2012).

4.2. Habitats An analysis of the biotopes of the Rapid Racerunner showed that the fixed sands dominated among the preferable habitats of *E. velox* in the eastern periphery of its species range, which generally confirmed Szczerbak's (1974) observations. Nevertheless, the species does not avoid the clay and debris substrates as was noted for the Ili Basin (Korelov, 1948; Ananjeva, 1976; our data) and Alakol Lake islands (Kubykin, 1975; our data), as well as gravel-loessic substrate which is typical for the Turpan Depression (our data).

4.3. Morphological variability We found a sexual dimorphism in the linear biometric characters of *E. velox* which was earlier shown by Ananjeva (1995, 2003) for Bakanas population. The males from the European populations also have a larger head size and longer tails and limbs (Scerbak [= Szczerbak], 1981). Scalation characters in our material did not demonstrate significant sexual differences. Previously, when describing the *E. v. velox* and *E. v. caucasia* subspecies, Szczerbak (1974) noted sexual dimorphism for Ventr. and Sq.cd. and in his later work (Scerbak [= Szczerbak], 1981) for Sq. and P.fm. The males in the Turkmen populations demonstrated dominance across all main diagnostic pholidosis characters (Shammakov, 1981). However, none of the authors specified the level of statistical significance of the differences.

Intraspecific morphological variability may be common in species inhabiting heterogeneous environments (Ghalambor *et al*., 2007), especially if the dispersal capability is relatively limited and the gene flow between populations is low (Slatkin, 1987). Our results indicate certain similarities and differences in the phynotype of the Rapid Racerunner populations inhabiting the intermountain and foothill basins in Southeast Kazakhstan and Xinjiang. The samples from Xinjiang (excluding the Turpan Depression) were characterized by above-average values for linear biometric characters, the number of scales across the torso, the scales around the 9-10th tail rings, as well as the guttural scales. The length of the head, torso and hind limbs of specimens from the Xinjiang populations confirm the general picture of cline variability for the linear biometric characters of *E. velox*. Most of the populations studied had differences in the dominant type of coloration patterns and scalation characters, not statistically supported in all cases. The noted originality in the morphology of the Xinjiang populations can be explained to some extent by the long-duration and distinct geographical isolation from the surrounding territories of Xinjiang (Murzayev, 1966). The Turpan and Alakol island lizards were characterized by the biggest differences in morphological features. The specimens of most populations (mainly the males) differed by high diversity of the dorsum coloration. The specimens in Alakol island and Shihezi populations were visibly uniform in dorsum coloration but such patterns were also found in other populations (Table 4). More than 70% of the Turpan specimens were recognized by uniform unique coloration pattern.

It is known that the coloration and the pattern of the Racerunners of the *Eremias* species (Kerzina, 1950; Szczerbak *et al*., 1993; Orlova and Terbish, 1997), including *E. velox* (Elpatjevsky, 1903; Dinesman, 1953; Szczerbak, 1974), correlate with the characteristics of the substrate. On the other hand, the character (i.e., percentage ratio of coloration patterns) is widely used in the intraspecific taxonomy of *E. velox* (Szczerbak, 1974; Shcherbak [= Szczerbak], 1975; Eremchenko and Panfilov, 1999a). As we know, the dominant type of biotope of the Racerunners from the studied populations was fixed sands with the surrounding clay plains. The racerunners from the Alakol islands, inhabiting the rubble-loam plains and sabulous-rocky slopes of low hills with a predominance of dark rocks, covered with desert dust, stand out in this regard. The racerunners had noticeably darker coloration, having the smallest size and most well-defined striped pattern on the backs of individuals of both sexes, compared to individuals from other populations. A similar striped pattern on the back was also noted by us among males from the Makanchi, Kuytun and Turpan populations; but the percentage of the specimens was low (Figure 7: 1; Table 4).

Along with some scalation characters (the low number of femoral pores and a higher percentage of individuals with an enlarged preanal scale), the particular traits of the Turpan specimens are manifested in their coloration pattern. At one time, this provided a reason for Bedriaga (1912) to identify, and later to Szczerbak (1974) to restore, the subspecies of *E.v. roborowski*. The Turpan Racerunners have a well-pronounced transverse-spotted coloration pattern of the back and very big blue spots on the sides. As far as we know from the literature, such a coloration pattern is extremely rare for *E. velox*: it was observed only among single cases from Turkmenistan, Uzbekistan and Kazakhstan (Szczerbak, 1974; Chirikova, 2004; our data). An unusual rust-brown coloration pattern of the upper torso of the Turpan Racerunners might be determined by a common substrate of the Turpan Depression represented by reddish concentrations of loess.

When exploring the morphological characters of *E.*

velox from the Turpan Depression, Wang *et al.* (2014) used a difference coefficient (Mayr *et al.*, 1953) and showed that none of the pholidosis characters reached the adopted indicator of subspecies differences. Nevertheless, Mayr and Ashlock (1991) indicated that inter-populational comparison should be carried out by taking into account a controversial picture of the morphological variability of the characters and the degree of isolation of the studied species. The Turpan Depression, which started its formation in the Cretaceous period, became significantly deeper and more isolated with the growth of the surrounding ridges in the Neogene (Murzayev, 1966). According to the results of molecular-genetic study (Liu *et al.*, 2014), the haplotypes of the Rapid Racerunner from the Turpan Depression constitute an independent basal clade, which is quite far from the haplotypes of the Junggar, Ili and Alakol depressions and the southern Balkhash region. An example, confirming the originality of the inhabitants of the isolated Turpan, is an independent evolving lineage (species) of the Roborowsk's Plate-tailed Gecko *Teratoscincus roborowskii* (Macey *et al.*, 1997; 1999; 2005).

Zoologists have long recognized that populations of a species occurring in different habitats may exhibit alternative forms (Mayr, 1942). Such morphological differences among habitats may confer selective advantages to individuals inhabiting physically different environments. In our opinion, the geographical isolation of *E. velox* in the Turpan Depression, the second lowest point in the world (−150 m) being separated before the Pleistocene (Wang, 1985), together with the morphological peculiarities and genetic distinctiveness of this form provide a solid basis to support its separate taxonomic status. Liu *et al.* (2014), using the concatenated cyt *b* and 12S rRNA gene sequences, found a significant mean genetic divergence (uncorrected *p*-distance) of 9.3% between *E. v. velox* and *E. v. roborowskii*. Since this work was submitted for publication, Liu *et al.* (2019) reported a phylogeogrpahical study complemented with ecological niche modeling on *E. velox* in arid Central Asia, which further provided the molecular and ecological niche bases to recognize the Turpan populations as a distinct genetic lineage. The split between *E. v. velox* and *E. v. roborowskii* is strongly supported. These two taxa show a deep divergence estimated approximately 3 million years ago based on mitochondrial DNA data (Liu *et al.*, 2019). The two subspecies are separated by the Tianshan Mountains (Liu *et al.*, 2014; 2019), which could act as a long-term barrier to gene flow and therefore promote speciation. The Tianshan Mountains as primary

driver for isolation have been identified also for other reptiles (Macey *et al.*, 2005; Shi and Zhao, 2011). Thus, considering the concordant molecular, ecological and morphological divergence, we suggest treating *E. v. velox* and *E. v. roborowskii* as distinct species, elevating the latter to species status. A full revision of the species complex, however, will necessitate inclusion of *E. v. borkini*, a recently described subspecies (Eremchenko and Panfilov, 1999a) not present in our study. As it is morphologically distinct from both *velox* and *roborowskii*, and separated from them by large mountains, it might also be characterized by a relevant genetic divergence. To decipher the evolutionary mechanisms that drive diversification in *E. velox* complex, further study is necessary to investigate how phenotypic variation responds to genetic and environmental variability in an explicit geographical framework.

References

Afifi A., Azen S. 1982. Statistical analysis: A computer oriented approach. Moscow, Russia: Mir Publishing House (In Russian)

Ananjeva N. B. 1976. The biotopic distribution of five species of desert lizards (*Eremias*, Sauria) of southern Balkhash region. Buyll Mosk Obshch Estestvoispyt, Biol Ser, 81: 65–72 (In Russian)

Ananjeva N. B. 1995. Comparative analysis of body size in five sympatric species of desert lacertas (*Eremias*, Sauria) of southern Balkhash region. Selevinia, 3: 3–10 (In Russian with English abstract)

Ananjeva N. B. 2003. Comparative analysis of limb proportions in five sympatric species of desert lizards (*Eremias*, Lacertidae, Sauria). Russ J Herpetol, 10: 140–144

Arnold S. J. 1983. Morphology, performance and fitness. Am Zool, 23: 347–361

Bedriaga J. V. "1905" 1907. Verzeichnis der von der central-asiatischen expedition unter stabs-kapitän W. Roborowski in den Jahren 1893–1895 gesammelten reptilien. Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St.-Pétersbourg, 10: 159–200 (In Russian)

Bedriaga J. V. 1912. Amphibien und reptilienna. Wissenschaftliche resultate der von N. M. Przewalski nach central-asien unternommenen reisen. Zool Theil, 3: 516–536 (In Russian and German)

Boulenger G. A. 1921. Monograph of the Lacertidae. Vol. 2. London: Trustees of the British Museum (Natural History), 308–314

Brushko Z. K. 1995. Lizards of the desert regions of Kazakhstan. Almaty, Kazakhstan: Konzhyk Publishing House, 231 pp (In Russian with English abstract)

Burtman V. S. 2012. Geodynamics of Tibet, Tarim, and Tien Shan in the late Cenozoic. Geotectonics, 3: 18–46 (In Russian with English abstract)

Chirikova M. A. 2004. Variability of *Eremias velox* Pallas, 1771 (Reptilia, Sauria) from Kazakhstan. Selevinia, 12: 24–34 (In Russian with English abstract)

Chirikova M. A. 2007. The lizards of the family Lacertidae in Kazakhstan (distribution, morphology, taxonomy). PhD Dissertation. Almaty, Kazakhstan: Institute of Zoology, 218 pp (In Russian with English abstract)

Dai X., Chen B., Zhang Z. W., Wang Y. Z. 2006. The morphological research of eight species of *Eremias* distributed in China (Lacertidae, *Eremias*). Acta Zootax Sinica, 31: 697–708 (In Chinese with English abstract)

Dai X., Zeng X. M., Chen B., Wang Y. Z. 2004. The research of the karyotypes of six species in the genus *Eremias* from China. Hereditas, 26: 669–675 (In Chinese with English abstract)

Dinesman L. G. 1953. Amphibians and reptiles of southeast of Turgai and northern Aral Sea regions. Trudy Instit geogr AN SSSR, 54: 384–422 (In Russian)

Elpatjevsky V. S. 1903. Amphibians and reptiles of islands and coasts of Aral Sea. Scientific Results of the Aral's Expedition. Izv Turkest otdel Russ Geogr Obsh, 4: 1–31 (In Russian)

Eremchenko V., Panfilov A. 1999a. Taxonomic position and geographic relations of a lacertid lizard *Eremias velox* from the Issyk-Kul lake depression, Tian Shan Mountains, Kyrgyzstan. Science and New Technologies, 1: 119–125

Eremchenko V. K., Panfilov A. M. 1999b. Taxonomic situation of multiocellated racerunner of the "*multiocellata*"-complex of Kyrgyzstan and neighbor China (Sauria: Lacertidae: *Eremias*). Science and New Technologies, 4: 112–124 (In Russian with English abstract)

Ghalambor C. K., McKay J. K., Carroll S. P., Reznick D. N. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Func Ecol, 21: 394–407

Hallgrímsson B., Hall B. K. 2005. Variation: A Central Concept in Biology. Burlington: Elsevier Academic Press, 592 pp

Kendall M., Stuart A. 1973. Statistical inferences and relationships. Moscow, Russia: Nauka Publishing House, Russia, 899 pp (In Russian)

Kerzina M. N. 1950. On the question of adaptivity of color variation of lizards. Bull Moscow Soc Naturalists, Biol Ser, 55: 32–36 (In Russian)

Kim Dzh. O., M'uyller P. U., Klekka U. R., Oldenderfer M. S., Bleshfild R. K. 1989. Factor, discriminant, and cluster analysis. Moscow, Russia: Finansovaya Statistika, 215 pp (In Russian)

Korablev P. N., Korablev M. P., Korablev N. P. 2011. The state of predatory mammal populations in the impact zone of the Kalinin Nuclear Power Plant as inferred from their phene pool. Russ J Ecol, 42: 288–295

Korablev M. P., Korablev P. N., Korablev N. P., Tumanov I. L. 2014. Polymorphism of the endangered European mink (*Mustela lutreola*, Carnivora, Mustelidae) population in the central forest reserve and neighboring areas. Biol Bull, 41: 620–628

Korelov M. N. 1948. Materials on vertebrates on the left bank of the Ili River (between the rivers Chilik and Charyn). Izv Acad Nauk KazSSR, Biol Ser, 8: 94–121 (In Russian)

Kozlov P. K. 1899. Report of the assistant to the chief of expedition of P. K. Kozlov. Works of Expedition of Russian Geogrraphy Society to Central Asia in 1893–1895 under the leadership of Roborowsky. Part II. Sankt-Petersburg (In Russian)

Kubykin R. A. 1975. Ecology-faunistic review on the reptiles of the islands of Alakol Lake (Eastern Kazakhstan). Izv Acad Nauk KazSSR, Biol Ser, 3: 10–16 (In Russian)

Kurdukov K. V. 1951. About fluctuations in the level of the Ala-kul lake. Voprosy Geographii, 24: 117-133 (In Russian)

Lande R. 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution, 30: 314–334

Ledermann W., Lloyd E. H. 1984. Handbook of applicable mathematics. Vol. 6. Statistics. New York: Wiley, 498 pp

Liu J., Ananjeva N. B., Chirikova M. A., Milto K. D., Guo X. 2014. Molecular assessment and taxonomic status of the Rapid Racerunner (*Eremias velox* complex) with particular attention to the populations in northwestern China. Asian Herpetol Res, 5: 12–25

Liu J., Guo X., Chen D., Li J., Yue B., Zeng X. 2019. Diversification and historical demography of the rapid racerunner (*Eremias velox*) in relation to geological history and Pleistocene climatic oscillations in arid central Asia. Mol Phylogenet Evol, 130: 244–258

Macey R. J., Ananjeva N. B., Wang Y., Papenfuss T. J. 1997. A taxonomic reevaluation of the gekkonid lizard genus *Teratoscincus* in China. Russ J Herpetol, 4: 8–16

Macey R. J., Fong J. J., Kuehl J. V., Shafiei S., Ananjeva N. B., Papenfuss T. J., Boore J. L. 2005. The complete mitochondrial genome of a gecko and the phylogenetic position of the middle eastern *Teratoscincus keyserlingii*. Mol Phylogenet Evol, 36: 188–193

Macey R. J., Wang Y., Ananjeva N. B., Larson A., Papenfuss T. J. 1999. Vicariant patterns of fragmentation among gekkonid lizards of the genus *Teratoscincus* produced by the Indian collision: A molecular phylogenetic perspective and area cladogram for Central Asia. Mol Phylogenet Evol, 12: 320–332

Mamedov G. M., Novikov I. S. 2015. Geomorphology of the Dzungarian Plain and its mountain frame. Geomorphology, 1:

88–100 (In Russian with English abstract).

Mayr E. 1942. Systematics and the origin of species, from the viewpoint of a zoologist. Cambridge: Harvard University Press, 334 pp

Mayr E., Ashlock P. D. 1991. Principles of systematic zoology. New York: McGraw Hill International Edition, 475 pp

Mayr E., Linsley E. G., Usinger R. L. 1953. Methods and principles of systematic zoology. New York: McGraw-Hill Book Company, 328 pp

Medeu A. R. 2010. The national atlas of the Republic of Kazakhstan: Vol. 3: Environment and Ecology. Institute of Geography, Nat Sci Tech Hold. "Parasat", 157 pp

Mullen L. M., Vignieri S. N., Gore J. A., Hoekstra H. E. 2009. Adaptive basis of geographic variation: genetic, phenotypic and environmental differences among beach mouse populations. Proc R Soc Lond B, 276: 3809–3818

Murzayev E. M. 1966. Nature of Xinjiang and formation of central Asian deserts. Moskow: Nauka Publ, 381 pp (In Russian)

Nikolsky A. M. 1905. Reptiles and amphibians of Russian Empire (Herpetologia rossica). Mémoires de l`Académie Impériale des Sciences de St. Pétersbourg. VIII Série. Classe physico-mathématoque, T. 17, N 1, 518 pp (In Russian)

Orlova V. F., Terbish Kh. 1997. True lizards (Lacertidae). In Ananjeva N. B., Munkhbayar Kh., Orlov N. L., Orlova V. F., Semenov D. V., Terbish Kh. (Eds), Amphibians and Reptiles of Mongolia. Reptiles. Moscow: KMK Scientific Press, 133–266 (In Russian)

Padial J. M., Miralles A., De la Riva I., Vences M. 2010. The integrative future of taxonomy. Front Zool, 7: 16

Rastegar-Pouyani E., Kazemi Noureini S., Rastegar-Pouyani N., Joger U., Wink M. 2012. Molecular phylogeny and intraspecific differentiation of the *Eremias velox* complex of the Iranian Plateau and central Asia (Sauria, Lacertidae). J Zool Syst Evol Res, 50: 220–229

Shammakov S. 1981. Reptiles of lowland Turkmenistan. Ashkhabad: Ylym, 309 pp (In Russian)

Shi L., Zhao E. M. 2011. A new gecko in the genus *Cyrtopodion* Fitzinger, 1843 (Reptilia: Squamata: Gekkonidae) from western China. Herpetologica, 67: 186–193

Shi L., Zhou Y. H., Yuan H. 2002. Reptile fauna and geographic divisions in Xinjiang Uygur Autonomous Region. Sichuan J Zool, 21: 152–156 (In Chinese with English abstract)

Sindaco R., Jeremčenko V. K. 2008. The Reptiles of western palearctic. 1. Annotated checklist and distributional atlas of the turtles, crocodiles, amphisbaenians and lizards of Europe, north Africa, middle east and central Asia. Latina, Italy: Edizioni Belvedere, 579 pp

Slatkin M. 1987. Gene flow and the geographic structure of natural populations. Science, 236: 787–792

Statsoft, 1999-2019. Statistica for Windows, version 10.0. Tulsa (OK): StatSoft Inc.

Szczerbak N. N. 1974. The palearctic desert lizards *(Eremias)*. Kiev: Naukova Dumka, 296 pp (In Russian)

Szczerbak N. N. 1975. Geographical variability and intraspecies taxonomy of *Eremias velox* Pall. 1771 (Reptilia, Sauria). Vestnik Zool, 6: 24–33 (In Russian with English abstract)

Szczerbak N. N. 1981. *Eremias velox* – Schneller Wustenrenner. In von Böhme W. (Ed), Handbuch der Reptilien und Amphibien Europas. Bd. 1. Echsen 1. Akademische Verlagsgesellschaft, Deutschland, 447–460 (In German)

Szczerbak N. N. 2003. Guide of the reptiles of the eastern palearctic. Florida: Krieger Publishing Company, 350 pp

Szczerbak N. N., Neruchev V. V., Okulova N. M., Orlova V. F. 1993. Taxonomy, geographic variation and interspecific structure. In Szczerbak N. N. (Ed), The Steppe-runner. Kiev: Naukova Dumka, 22–34 (In Russian)

Wan L., Sun S., Jin Y., Yan Y., Liu N. 2007. Molecular phylogeography of the Chinese lacertids of the genus *Eremias* (Lacertidae) based on 16S rRNA mitochondrial DNA sequences. Amphibia-Reptilia, 28: 33–41

Wang H. Z. 1985. Atlas of the paleogeography of China. Being, China: Cartographic Publishing House, 143 pp (In Chinese and English)

Wang Y., Autumn K. 1990. Home range size and spatial distribution of *Phrynocephalus przewalskii*, *P. axillaris* and *Eremias velox*. In Zhao E. (Ed), From Water onto Land – A Volume Issued to Commemorate the 90th Birthday of the Late Professor Liu Cheng-zhao. Beijing, China: Forestry Publishing House, 125–132 (In Chinese with English abstract)

Wang Y., Zhou L., Shi L. 2014. Scalation variation and subspecies classification status of rapid racerunner (*Eremias velox*) in Xinjiang. Sichuan J Zool, 33: 13–18 (In Chinese with English abstract)

Yao C. 1983. Lizard of Gansu province. Acta Herpetologica Sinica, 2: 66–67 (In Chinese)

Zaychikov V. T. 1964. Physical geography of China. Moscow: Mysl' Publ., 740 pp (In Russian)

Zhao K. T. 1985. An investigation of the lizards of Xinjiang Uygur Autonomous Region. Acta Herpetologica Sinica, 4: 25–29 (In Chinese with English abstract)

Zhao K. T. 1999. *Eremias velox* (Pallas, 1771). In Zhao E. M., Zhao K. T., Zhou K. Y., *et al.* (Eds), Fauna Sinica, Reptilia. Vol. 2. Beijing, China: Science Press, 238-241(In Chinese)

Zhivotovsky L. A. 1982. Indicators of population variation in polymorphic characters. In Yablokov A. V. (Ed), Phenetics of Populations. Moscow, Russia: Nauka Publishing House, 38–69 (In Russian)

Appendix 1

List of Specimens

IZKAZ (84): 1, Bakanas–5/67–69, 72, 282, 283–286, 356, 358, 361; 2, Charyn–118/1304–1307, 1309, 1339–1341, 1403–1406, 1462–1469; 3, Alakol Lake, 1970–397/4722–4726, 4728, 4732, 4734, 4735, 4737–4741, 4773; 899/1–3, 6, 7, 10; 4, Alakol Lake, 2015–909/1–14; 5, Makanchi–303/3223–3227, 3230, 3232, 3234–3236, 3239–3241, 3243, 3246, 3247, 3249

CIB (51): 6, Kuytun–Guo2182–Guo2187; 7, Shihezi–Guo2173–2175, 2196–2206; 8, Urumqi–Guo2066 E, Guo2138, Guo2142–Guo2144, Guo2151–Guo2154, Guo2156, Guo2161, Guo2162; 9, Turpan Depression–WGXG08203–WGXG08208, WGXG08258–WGXG08264, LJE0707001–LJE0707006